Effects of Extended Photoperiods and Light Intensities on Growth, Sexual Maturation and Tissue Water Content of Atlantic Cod (*Gadus morhua*) in Sea Cages

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Effects of extended photoperiods and light intensities on growth, sexual maturation and tissue water content of Atlantic cod (*Gadus morhua*) in sea cages

by

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ABSTRACT

Trippel, E.A., Neil, S.R.E., Puckrin, O.A., Dickinson, L. and Powell, F. 2011. Effects of extended photoperiods and light intensities on growth, sexual maturation and tissue water content of Atlantic cod (*Gadus morhua*) in sea cages. Can. Tech. Rep. Fish. Aquat. Sci. 2925: iv+44 p.

Mariculture of Atlantic cod (*Gadus morhua*) in the Bay of Fundy was initiated in the early 2000s and early maturation has been a persistent problem since its inception. The objectives of the present study were to evaluate, over separate two-year periods, whether 20 and 24 h light exposure compared to natural photoperiod in sea cages will (i) increase body growth, (ii) halt or delay sexual maturation, (iii) influence investment in reproductive tissue as reflected in gonad weight, and (iv) affect seasonal levels of water content in muscle and liver tissue of Atlantic cod. A positive growth response to extended daylength (20 and 24 h light) was observed, though these light treatments did not influence the incidence of sexual maturation of either sex. The greater light intensity used at the Fundy site (4.8 kHz) compared to Kelly Cove (1.6 kHz) also did not reduce incidence of maturity. Proportion of fish sampled that were mature was often >90%. Immature cod of each gender were reported to grow at slower rates than mature cod and this trend was consistent across all treatments and multiple years. Implementation of extended daylength did, however, result in delaying attainment of sexual maturation by ~3 months. Of particular note is the lower reproductive investment (i.e., female GSI values) observed after two years of 20 h daily illumination. Water content of fillet muscle was surprisingly quite constant throughout the study with only minor variation. In the Fundy site, percent water content of muscle tissue of adult females commonly ranged from 78-83%, regardless of light treatment. Water content of muscle of immature females ranged from 80-83%. Spawning females occasionally exhibited the highest water content over other adult females (+5-10% at Kelly Cove; +2-3% at Fundy site). Hepatosomatic index was greatest during the winter/spring period and for pre-spawning fish. Investment in liver tissue was lowest for immature fish. Water content of liver tissue ranged from 25-50%. Our results suggest the use of extended daylength to improve growth and change the timing and investment in reproduction holds some promise for Atlantic cod mariculture. Light measurements verified the inability of artificial light to equal the much stronger ambient light cycle further indicating the difficulty in influencing fish physiological cycles compared to lab experiments with light tight lids.

RÉSUMÉ

Trippel, E. A., Neil, S. R. E., Puckrin, O.A., Dickinson, L. and Powell, F. 2011. Effects of extended photoperiods and light intensities on growth, sexual maturation and tissue water content of Atlantic cod (*Gadus morhua*) in sea cages. Can. Tech. Rep. Fish. Aquat. Sci. 2925: iv+44 p.

L'élevage de la morue franche (*Gadus morhua*) dans la baie de Fundy a commencé au début des années 2000. L'arrivée à maturité précoce des individus mis en élevage est un problème qui perdure depuis le début de cette activité. La présente étude a pour objectif d'établir, au cours de deux périodes distinctes de deux ans, si une exposition à la lumière de 20 heures et de 24 heures en comparaison de la photopériode naturelle dans des cages mouillées en mer (i) mène à une plus grande taille des individus, (ii) stoppe ou retarde la maturité sexuelle, (iii) module l'investissement dans le développement des organes reproducteurs tel que reflété dans le poids des gonades et (iv) a un effet sur les niveaux saisonniers de teneur en eau dans les muscles et le foie. Nous avons observé un taux de croissance positif en réponse à une durée du jour prolongée (20 heures et 24 heures), bien que ces traitements lumineux n'ont pas agit sur l'incidence de la maturité sexuelle chez les deux sexes. La plus forte intensité lumineuse utilisée au site de la baie de Fundy (4,8 kHz) en comparaison du site de Kelly Cove (1,6 kHz) n'a pas réduit non plus l'incidence de la maturité sexuelle. La proportion d'individus échantillonnés qui avait atteint la maturité était souvent supérieure à 90 %. Le taux de croissance des morues immatures de chaque sexe était inférieur au taux chez les morues matures, et cette tendance était la même pour les divers traitements et les années. L'application d'une durée du jour prolongée a toutefois mené au retard de l'atteinte de la maturité sexuelle par environ trois mois. Un plus faible investissement dans la reproduction (c.-à-d. les valeurs de l'IGS des femelles) a été notamment observé après deux ans d'éclairement lumineux de 20 heures. La teneur en eau des filets est demeurée étonnamment assez constante tout au long de l'étude et n'a que peut varié. Au site de la baie de Fundy, la teneur en eau (%) des muscles chez les femelles adultes allait habituellement de 78 à 83 %, indépendamment du traitement lumineux, alors que la teneur en eau des muscles chez les femelles immatures allait de 80 à 83 %. À l'occasion, les femelles en fraie montraient la teneur en eau la plus élevée par rapport aux autres femelles (+ 5-10 % à Kelly Cove; + 2-3 % au site de la baie de Fundy). L'indice hépato-somatique était le plus élevé durant la période hiver-printemps, et cela chez les individus prégénésiques. L'investissement dans le développement du tissu hépatique était le plus faible chez les individus immatures. La teneur en eau du tissu hépatique allait de 25 à 50 %. Nos résultats portent à croire que l'utilisation d'une durée du jour prolongée en vue d'accroître le taux de croissance et de changer le moment de la reproduction et l'investissement dans la fraie est prometteur dans une certaine mesure pour l'élevage de la morue franche. Les mesures de l'intensité lumineuse ont permis de vérifier que la lumière artificielle n'égale pas le cycle lumineux naturel, nettement plus intense, ce qui souligne la difficulté de moduler les cycles physiologiques du poisson en comparaison d'expériences en laboratoire faisant appel à des bassins étanches à la lumière.

INTRODUCTION

Over the previous 20-25 years, mariculture of Atlantic cod (*Gadus morhua*) has been initiated in Canada, Norway, USA, Iceland, Ireland, Scotland, and the Faroe Islands (Rosenlund and Skretting 2006). In an effort to attain commercialization, a number of culture limitations have been observed in nearly all life history stages, including grow-out in sea cages. One of the as yet unsolved problems is the young ages and small body sizes at which cod achieve sexual maturation (Taranger et al. 2006). Onset of maturation may occur as early as in the first year of life in males and second year in females. Given residency time in sea cages to harvest in North America is currently three years at best (Chambers and Howell 2006; Garber et al. 2010; Tosh et al. 2010) a significant investment in reproduction by these animals occurs annually.

The perceived negative consequences to the fish farmer of sexual maturation, although not rigorously quantified are (i) a trade-off in energetic investment between soma and gonad which potentially compromises the scope for somatic growth, (ii) changes in fillet quality and whether the water content increases such that they become more 'jellied' with spawning, and (iii) the physiological strain involved in spawning that elevates mortalities and results in significant losses for farmers within a year or more of harvest. Apart from the threat of escaped fish, a negative consequence from an ecological perspective and of interest to farmers and those monitoring wild cod stocks, is that natural spawning by cod in sea pens has been observed and the embryos that drift through the cage mesh could possibly survive to adulthood and reproduce with local wild fish (i.e., genetic introgression of farmed and wild fish) (Jørstad et al. 2008).

Manipulation of photoperiod has been successfully used to halt gametogenesis in fishes, especially Atlantic salmon (*Salmo salar*) (Porter et al. 1999; Harmon et al. 2003). Use of submerged lights at night to illuminate sea cages acts to block the ability of fish to sense the seasonal changes in daylength, particularly the autumn shortening of daylight which has been experimentally demonstrated to trigger onset of sexual maturation (Taranger et al. 1999, 2010; Davie et al., 2007). Implementation of an extended fixed daylength, as an alternative to continuous light, can also possibly act to mask changing daylength such as exposing fish to 16 h of light and 8 h of darkness each day (Imsland et al. 1997). It is believed that animals would cue on the fixed, extended daylength and thereby not undergo a physiological hormone response to mature that normally accompanies the shortening of daylength associated with autumn. This method supposedly would be cost saving as less energy would be required to generate light over a single evening.

Mariculture of Atlantic cod in the Bay of Fundy was initiated in the early 2000s and early puberty has been a persistent problem since its inception (Trippel et al. 2008). Photoperiod manipulation, by using 24 h light exposure, has been successfully deployed at a commercial level to block sexual maturation of Atlantic salmon in the Fundy Isles region (Peterson and Harmon, 2005) and it was of interest to see if a similar favourable response could be achieved for cod.

The objectives of the present study were to evaluate whether 20 and 24 h light exposure compared to natural photoperiod in sea cages will (1) increase body growth, (2) halt or delay

sexual maturation, (3) influence investment in reproductive tissue as reflected in gonad weight, and (4) affect seasonal levels of water content in muscle and liver tissue of Atlantic cod.

MATERIALS AND METHODS

Two mariculture cage sites operated by Cooke Aquaculture Inc. in the Fundy Isles region (45°N latitude, 67°W longitude) were used for this study: (i) Kelly Cove near L'Etete Passage (Green Point Lighthouse) (2005-2007) and (ii) Fundy site near Back Bay, New Brunswick (2007-2009) (Figs. 1-3). At the Kelly Cove site, two 70 m polar circle cages were deployed for a two year experiment, one cage at natural photoperiod (NP) and the other under 24 h light. Cage characteristics were circumference 70 m, diameter 21.2 m, depth 7.5 m, volume 2,659 m^3, mesh size 2.25 inches (5.7 cm), anti-predator bird net mesh size 6 inches (15.2 cm), and absence of a shade cloth. The lit cage had six 400 W submerged metal halide lights (Aquastar Aquaculture Marine Systems) that were turned on in July 2005 and were powered by a land-based electrical supply as the site was close to shore. Lights were distributed in one horizontal plane at a depth of 2 m such that the six lights were spaced equally apart along the circumference of a 13 m diameter circle pattern centred in the cage. The depth of water, at normal low tide, between the bottom of the cage and the ocean floor was ~3.3 m.

Cod in each cage at Kelly C[illegible] were progeny of wild broodstock collected by commercial fishermen using jig fishing in [illegible]e 2003 on the inshore spawning grounds near Portsmouth, New Hampshire (45-55 m depth, NAFO Subdivision 5Y) and held at GreatBay Aquaculture Inc. where they were stripped shortly after being brought to the facility. Larvae and juvenile cod at GreatBay were maintained at 24 h light prior to stocking as juveniles (~40 g) in May 2004. Fish in cages were subjected to natural photoperiod conditions for 14 months prior to turning on lights in July 2005 (~20,000 fish were present per cage at onset of the trial; 7.5 fish or 0.30 kg per m^3). Periodic access to fish samples was provided by Cooke Aquaculture Inc. in order to monitor a number of body attributes over the duration of the experiment. Sampling months numbered between 10 and 14 for each cage and spanned the period January 2006 to September 2007 (21 months). Approximately 15-20 cod per cage were made available on each sampling date. Body characteristics recorded were total length (±0.1 cm), body weight (±1 g), carcass weight (±1 g) (i.e., body weight without internal organs; head on gutted), sex, gonad weight (±0.1 g), gonadal stage of development (after Tomkiewicz et al. 2002) and liver weight (±0.1 g). Immature and mature fish were categorized according to Tomkiewicz et al. (2002) to estimate proportion mature. Immature fish were represented by I Juvenile. Adult gonadal stages were categorized into three groups to simplify representation of the spawning state: *Pre-Spawning*: II Preparation, III Ripening 1 (oocyte recruitment), IV Ripening 2 (late vitellogenesis); *Spawning*: V Spawning 1 (initiation of spawning), VI Spawning 2 (main spawning period), VII Spawning 3 (cessation of spawning), and *Post-Spawning*: VIII Regeneration 1 (spent), IX Regeneration 2 (resting and spawning omission) and X Degeneration (reduced fertility). These stages represented attainment of sexual maturity. Maturity data collected over the duration of the experiment were pooled per treatment, and estimates of percent mature were generated by sex. Additionally, the mean percent occurrence of each adult stage was plotted to examine for seasonal changes in spawning condition for each treatment.

Gonadosomatic index (GSI) (gonad weight/body weight)*100 and hepatosomatic index (HSI) (liver weight/body weight)*100 were calculated. Estimates of percent water content of white muscle (fillet) and liver were made. One sample (~1-2 g) from each of muscle and liver were removed from each fish. These were weighed (±0.001 g) on pre-weighed foil dishes, dried in an oven at 80°C for two days until constant weight was achieved, and weighed again to estimate percent water content of each tissue per individual. Mean and standard error of data collected per month were estimated for each light treatment and plotted to examine for seasonal trends in body characteristics.

At the second mariculture site, Fundy site near Back Bay, lights were installed into square steel cages and polar circle cages in October 2007 for a two year experiment. Nine steel cages were used in this second trial, each cage being 20 m x 20 m x 7 m (depth) (2,800 m^3) as well as four 70 m polar circle cages of the type used at Kelly Cove. The same mesh sizes were used in these cages as for Kelly Cove. The depth of water, at normal low tide, between the bottom of the cages and the ocean floor was ~10.5 m.

The lighting array at Fundy was more intense than at Kelly Cove and configured somewhat differently. In each lit cage, six 800 W lights (Aquastar Aquaculture Machine Systems) (Fig. 4) were placed such that three lights were in one horizontal plane and the other three in another horizontal plane. These three-sided, horizontal planes had dimensions of 7 m between each light within a plane. The upper plane was 1.6 m and the second 3.6 m from the water's surface.

Natural photoperiod and extended daylength (20 h) at this high light intensity were investigated at the Fundy site. The 20 h period resulted in cod receiving artificial light from 0400-0000 h (i.e., darkness was midnight to 0400 h). Cod for the Fundy site were produced by GreatBay Aquaculture Inc. in December 2005 from gametes of winter-spawning, wild collected broodstock in much the same manner as done for the Kelly Cove fish and transferred as 6-10 g juveniles from Portsmouth, NH to the L&J site in Back Bay in July and August 2006. At GreatBay, juvenile cod were subjected to 24 h light prior to transfer to the L&J site as this is normal procedure to improve growth before being stocked to sea cages (Trippel and Neil, 2003). They were reared at the L&J site under natural photoperiod prior to transfer to the 11 cages at the nearby Fundy site in July and August 2007. Approximately 16,000 to 22,000 fish were present in each cage at the Fundy site at the initiation of artificial light exposure, though subsequent knowledge of numbers of fish per cage through the course of the trial was unavailable. Cages were monitored beginning in October 2007 as follows: natural photoperiod: three square cages and two polar circles, 20 h light: four square cages and two polar circle cages. The same set of body measurements, tissue samples, statistical analysis and graphical presentation of data were prepared for fish of the Fundy site as they were for Kelly cove.

At Fundy site, more so than at Kelly Cove, restricted sampling occurred throughout the experimental period due in part to industry restrictions in gaining access to large numbers of fish from each cage and available technical support. Approximately 12-15 cod were made available from selected cages on the sampling dates. This inability to repeatedly sample the same cages on each sampling date violates assumptions associated with statistical testing and so results were limited to comparisons of mean, standard error and range. Additionally, at Kelly Cove, no replication of treatment was conducted. Despite these limitations, the rarity of receiving access

to farmed cod in experimental light trials, particularly from industry partners, substantiates the collating and reporting of the study results within this context. Lack of replication in farmed fish light trials is not unique to this study (e.g., Taranger et al. 2006) as the amount of infrastructure needed is often difficult to obtain compared to, for example, tank-based experiments (Treasurer et al. 2006).

SCUBA divers assisted with gathering light readings (several hours after sunset) from different locations within cages at each of the two experimental sites. Light readings were recorded in lux using a *SeeBrite*™ Underwater Illumination Intensity Meter (Serial number SPQA 4158; Integrated Aqua Systems, Escondido, CA). Measurements to assess daytime light intensity were recorded during mid-day (noon) at various depths at the wharf of the St. Andrews Biological Station on a sunny and cloudy day on September 1 and 7, 2010 (respectively) and on an overcast day (November 15, 2010) at the same sea cage and positions where night-time readings were recorded at the Fundy Site. Monthly water temperature data were provided by Cooke Aquaculture Inc. for each site. Fish at each site were fed daily during daylight, except for at extreme low water temperatures, at which time feeding was reduced to three times per week. To control biofouling, cage nets were changed annually. Cod were occasionally observed to forage on mussels and other organisms growing on the inside of the netting.

RESULTS

NATURAL AND ARTIFICIAL LIGHT INTENSITY

At the St. Andrews Biological Station, daylight illuminations at noon on a sunny, cloudless day and overcast day (grey clouds, light rain) (September 1 and 7, 2010, respectively) are shown from the water's surface to 7.5 m depth (Table 1). Light intensity at the surface and transmission below the surface were markedly higher on the sunny compared to the rainy, overcast day.

Table 1. Light intensity (lux) at various depths at the St. Andrews Biological Station wharf under sunny (September 1, 2010) and cloudy (September 7, 2010) conditions measured at mid-day.

	Light Intensity (lux)	
Depth (m)	Sunny	Cloudy
Surface	181,362	121,556
1.5	168,396	87,790
3.0	146,411	59,576
4.5	126,311	22,784
6.0	112,436	2,051
7.5	113,316	1,096

Kelly Cove Site

A single lit 70 m polar circle cage (24 h illumination) was comprised of six 400 W submerged lights. A photograph showing night illumination from the surface indicates an impression of the lit cage conditions (Fig. 5). Light levels at night ranged from 160 lux in the centre of the centrally located ring of lights suspended at 2.0 m depth to 9 lux at the middle of the cage bottom (7.5 m) (Fig. 6; Table 2). Light levels ranged from 22-30 lux along the cage sides (Table 2). The monitored unlit cage was of the same dimensions as the lit cage. Neither of these two cages were covered with a shade cloth, hence bright daylight would still induce some diel differences in light intensity in the lit cage (both were covered by 6 inch (15.2 cm) mesh anti-bird predatory nets; Fig. 5). As a comparison, light intensity at 3 m depth on a sunny day off the St. Andrews Biological Station wharf (146,411 lux at 3 m) and at night in the cage (160 lux at 2 m) differed by nearly three orders of magnitude (915-fold) (Tables 1 and 2).

Table 2. Light intensity (lux) of illuminated cages at night at various positions (stations) within a 21.2 m diameter polar circle cage at Kelly Cove and a 20 m x 20 m square steel cage at the Fundy site, as well as outside of the Fundy cage.

Kelly Cove			**Fundy**						Distance from Cage	
Depth	Center (1)	Side (2)	Depth	Center (1)	Mid (2)	Side (3)	Corner (4)	Side (5)	2m (6)	4m (7)
Surface	-	-	Surface	-	-	4	3	10	1	1
2m	160	30	0.9m	163	124	6	3	13	1	<1
4m	53	25	1.8m	203	31,887	6	4	21	1	<1
6m	19	22	3.6m	7	6,913	6	15	10	1	<1
Cage Bottom Depth at Bottom	9 7.5m	-	Cage Bottom Depth at Bottom	3 6.4m	271 7.3m	3 5.2m	30 5.2m	10 5.2m		

Table 3. Light intensity (lux) measured at mid-day at various positions (stations) within and outside a 20 m x 20 m unlit square steel cage at Fundy site on November 15, 2010 (see also Fig. 6).

Fundy						Distance From Cage		
Depth	Center (1)	Mid (2)	Side (3)	Corner (4)	Side (5)	Depth	2m	4m
Surface	148,885	183,943	162,719	153,495	168,340	Surface	190,599	191,793
0.9m	149,007	167,083	141,280	141,195	142,182	1.52m	162,867	165,981
1.8m	79,684	107,964	39,803	59,277	89,554	3.04m	131,350	131,285
3.6m	28,532	52,821	11,226	30,615	33,150	4.56m	103,596	95,105
Cage Bottom	3,754	14,479	1,942	7,888	17,716	6.08m	50,374	50,815
Depth at Bottom	6.4m	7.3m	5.2m	5.2m	5.2m	7.60m	17,909	24,540

Fundy Site

Table 2 shows night illumination of one of the six square lit cages. Despite the use of 4.8kW of light, a large difference in light intensity at depth existed during night and day (Tables 2 and 3). The procedure of placing lights in two planes of three bulbs each and the higher wattage (4.8 kW vs. 2.4 kW) resulted in greater light intensity for lit cages at the Fundy compared to Kelly Cove site. Light readings were recorded at five locations (stations) within the square cage site and at two stations external to the cage site (Fig. 6). Light intensity was greatest nearest to the light source peaking at 31,887 lux at a bulb (depth 1.8 m) and diminished rapidly towards the cage perimeter where at just inside the cage sides it ranged from 4 to 21 lux (depth ranges 0 to 3.6 m). Already at 1 m from the cage side the light intensity at night was nearly nil (1 lux) indicating artificial light did not distribute to any neighbouring cages in the experimental trials (Figs. 2 and 3). The intensity of light at the bottom of the sea cage (central location, depth 7.3 m) was at maximum 271 lux (3.3 m directly below an 800W bulb; 6.5 m occurred from a bulb to the nearest cage side). Given there were three bulbs situated ~3.3 m from the cage bottom, it would appear that based on bulb light distribution patterns the cage bottom light at most other locations would be significantly less than 271 lux. At one of the corners (depth 5.2 m) the light intensity was 30 lux.

State of net side biofouling, as observed by the SCUBA diver, at time of night light reading was judged to be medium from 0-2 m depth and none to minor below 2 m. Light intensity external to the cage side was recorded and found to be very low (1 lux or less). Hence, the greatest light intensity presumably exiting the cage occurred at points closest to the six bulbs (the depth between the cage bottom and the sea floor was commonly ~10.5 m at the Fundy site). Moreover, light distribution presumably was more evenly distributed (horizontal perspective) through a cage during daylight compared to that produced by the bulbs. During daylight, divers noted cod were closer to cage bottoms and perhaps there was a range of light experienced among individual cod within a cage depending on the horizontal layer they positioned

themselves in (i.e., some fish may have used the shadow of fish above them to avoid daytime light intensity). Fish were noted by the diver to be more evenly spread about a cage at night when it was lit compared to the benthic daytime distribution (R. Bosien, pers. comm.). Note that the light distribution towards the cage periphery would be somewhat different for a polar circle compared to a square cage.

Measurement of daytime light penetration within the cage was made by a SCUBA diver on November 15, 2010 (cloudy, overcast day) and recordings were made in the same locations as at night (Tables 2 and 3). Light readings were similar between those recorded on November 15 at the cages in daytime and those in early September on the sunny day at the St. Andrews Biological Station wharf.

Furthermore, light intensity at 3 m depth during daytime at the cage (52,821 lux at 3.6 m; Station 2) and at night in the cage (6,913 lux at 3.6 m; Station 2) differed by 7.6-fold, though nearby at Station 3 (cage side) it differed by 1,871-fold (11,226 and 6 lux at 3.6 m, respectively). Thus, great heterogeneity in light intensity existed within a lit cage, even when 6 bulbs generating 4.8 kW in total were deployed.

WATER TEMPEATURE

Kelly Cove and Fundy Sites

The most pronounced thermal feature was the strong seasonal cycling evident in water temperatures for these sites. Monthly average water temperatures (near surface) at Kelly Cove and Fundy sites are shown in Figure 7. Marked seasonal changes are evident with Kelly Cove being slightly colder on average. In 2007, the only year in which measurements for both sites were available, the Kelly Cove site was cooler by ~0.8°C on average over the entire year compared to Fundy (Table 4). This difference was mainly due to the summer temperatures reaching 11°C at Kelly Cove in 2007 compared to ~13°C at the Fundy site. Peak water temperature occurred in August-September and attained up to ~13°C at each site over four years of monitoring and low water temperature occurred in February-March reaching ~2°C for which three months temperatures were <3°C. The tidal amplitude in the area (~5.5 m) acted to mix water vertically though at times presumably some difference in water temperature existed between the surface and bottom of the cage, particularly in summer during slack tide when the top 1-2 m would be warmer.

Table 4. Mean annual water temperatures (°C) at Kelly Cove and Fundy cage sites from 2006 to 2009.

Year	Kelly Cove	Fundy
2006	7.89	-
2007	6.63	7.39
2008	-	7.65
2009	-	7.19

BODY LENGTH

Kelly Cove Site

The length of NP adult females increased from 51 to 66 cm and the length of 24 h females from 55 to 70 cm over the period January 2006 to June 2007 (Fig. 8). Immature NP females, at each sampling month, were shorter than adult females ranging from 38 to 56 cm.

The length of NP adult males increased from 47 to 59 cm and the length of 24 h males from 49 to 63 cm over the period January 2006 to June 2007 (Fig. 8). Immature males were only sampled in January 2006 and were smaller than mature males.

Fundy Site

The length of NP adult females increased from 38 to 53 cm and the length of 20 h adult females from 33 to 62 cm over the period November 2007 to September 2009 (Fig. 9). At each sampling month, immature females were shorter than adult females ranging from 27 to 41 cm, except for 20 h in November 2007 when the immature females were very similar in size to mature females.

The length of NP adult males increased from 39 to 55 cm and the length of 20 h adult males increased from 35 to 61 cm over the period January 2006 to June 2007 (Fig. 9). At each sampling month, immature males were shorter than adult males.

CARCASS WEIGHT

Kelly Cove Site

The carcass weight of NP adult females increased from 1,250 to 2,250 g (80%) over the period January 2006 to June 2007, whereas the carcass weight of 24 h adult females increased from 1,500 to 2,400 g (60%) over the same time period (Fig. 10). Immature females were very similar to or weighed less than adult females.

The carcass weight of NP adult males increased from 1,000 to 1,750 g (75%) over the period January 2006 to June 2007, whereas the carcass weight of 24 h adult males increased from 1,150 to 2,200 g (91%) over the same time period (Fig. 10). Few immature males were sampled and these weighed less than mature males, often by a considerable amount (one-third the carcass weight).

Fundy Site

The carcass weight of NP adult females increased from 500 to 1,400 g (180%) from November 2007 to September 2009, whereas the carcass weight of 20 h adult females increased from 300 to 1,800 g (500%) over this same time period (Fig. 11). At each sampling month, immature females weighed less than adult females ranging from 175 to 350 g (except for 20 h in

November and December when the immature females were very similar in carcass weight to mature females); a 3-fold difference was often observed between immature and mature females.

The carcass weight of NP adult males increased from 575 to 1,500 g (161%) from November 2007 to September 2009, whereas the carcass weight of 20 h adult males increased from 375 to 1,850 g (393%) over this same time period (Fig. 11). At each sampling month, immature males weighed less than adult males ranging from 200 to 375 g; a 3-fold difference was often observed between immature and mature males.

PROPORTION SEXUALLY MATURE

Kelly Cove and Fundy Sites

In Kelly Cove, NP and 24 h light treatments resulted in 92-100% maturity in 2006 and 2007 (Table 5). In Fundy site, few fish were sampled in 2007 but after two years of illumination, proportion mature ranged from 94-100% of each sex in 2008 and in 2009 all fish sampled of either sex were mature. These data indicated photoperiod or light intensity apparently did not affect incidence of sexual maturation of either sex in Kelly Cove and Fundy sites even after successive years of illumination.

Table 5. Proportion of mature and immature female and male Atlantic cod in each treatment sampled at Kelly Cove (KC) (NP- natural photoperiod, 24 h- 24 hour light) and Fundy (NP- natural photoperiod, 20 h- 20 hour light) cage sites from 2006 to 2009.

Site	Year	Treatment	Sex	N Total	N Mature	N Immature	%Mature
Kelly Cove	2006	24 h	F	130	120	10	92.3
			M	61	59	2	96.7
		NP	F	49	46	3	93.9
			M	42	42	0	100
	2007	24 h	F	73	70	3	95.9
			M	44	44	0	100
		NP	F	18	17	1	94.4
			M	18	18	0	100
		Total	F	270	253	17	93.7
		Total	M	165	163	2	98.8
Fundy	2007	20 h	F	19	8	11	42.1
			M	8	7	1	87.5
		NP	F	8	4	4	50
			M	7	0	7	0
	2008	20 h	F	83	79	4	95.2
			M	100	96	4	96
		NP	F	83	78	5	94
			M	77	74	3	96.1
	2009	20 h	F	14	14	0	100
			M	12	12	0	100
		NP	F	10	10	0	100
			M	15	15	0	100
		Total	F	217	193	24	88.9
		Total	M	219	204	15	93.2

GONADAL DEVELOPMENTAL STAGES AND GONADOSOMATIC INDEX

Kelly Cove Site

Females

NP females were in spawning condition in April to June 2006, whereas at 24 h light females in spawning condition were observed in July-September indicating about a 3 month delay compared to NP (Fig. 12). In the second year, NP females were in spawning condition from March to May and 24 h light females were in spawning condition from March to August 2007, indicating maturation was no longer delayed for some fish at 24 h light.

NP females exhibited low GSI values in 2006, whereas those under 24 h light had higher values and reflected in part the prolonged pattern of attaining and maintaining the ripe state through and after the typical winter-spring spawning period (Fig. 13). Female GSI values were often

between 4-7% with some values being higher (Fig 13). In 2007, GSI values for NP females rose considerably from a year earlier to nearly 19% in April-June, and GSI values for 24 h light females ranged from 7-16% when in spawning condition with some individuals being in this state in September.

Males

NP males were in spawning condition in April 2006, whereas at 24 h light spawning condition extended from March to September 2006, with a high proportion of males releasing milt observed in July and September which is in agreement with the 3 month delayed maturation observed in females under 24 h light (Fig. 12). In the second year, NP males were in spawning condition in March and 24 h light males were in spawning condition from April to June 2007 with all males spent in August.

NP males exhibited GSI values of ~7% from January to May 2006, whereas those under 24 h light exhibited GSI values of this magnitude until October 2006 with many in spawning condition (Fig. 13). In 2007, GSI of NP males peaked in March and those at 24 h light exhibited their highest GSI's in April with declines in both light treatments in June indicating adherence to a more normal winter/spring spawning period after two years of 24 h illumination for this sex.

Fundy Site

Females

NP females were in spawning condition from January to April 2008 and 20 h females from January to July 2008 (Fig. 14). This is evidence that 20 h light prolonged female spawning into summer compared to NP as ~70% of females sampled at 20 h light in July were ripe and running. In the second year, NP females were in spawning condition from December to April and 20 h light females in January though a large percentage of ripening females existed at 20 h light in April 2009.

NP spawning females exhibited GSI values up to 23% in January but were commonly between 5-7% for pre-spawning or spawning females until April 2008 (Fig. 15). At 20 h, female spawning GSI maintained levels of 8-15% from January to July providing further support of delayed spawning for this treatment. In the second year, NP females attained GSI values of 10-13% in December to April, whereas 20 h females interestingly had very low GSI values of <4% from December to August including those in spawning condition. Consequently, 20 h light seemed to be effective in reducing gonadal investment after the second fall/winter of night illumination. This prolonged effect into the second year was not observed for 24 h females held at Kelly Cove. Immature females had GSI values of <1% and post-spawning females between 2-4% across all treatments.

Males

NP males were in spawning condition from January to April and 20 h light males from January to July, 2008 (Fig. 14). This is evidence that 20 h light prolonged male spawning into summer

compared to NP. In the second year, NP males were in spawning condition from December to April, 20 h males in December with a large proportion ripening in December and April and evidence of summer spawning by presence of ripe males in August, 2009. This is evidence that the second year of lights for males, compared to females, was less effective at inducing a continued delay in sexual maturation.

NP males exhibited GSI spawning values of 3-4% in January-April, which were also observed for 20 h males from January-July. A very low GSI of <1% was observed for spawning males in July indicating that 20 h light was more effective at delaying the male spawning period in this first year (Fig. 15). In the second year, NP males had GSI values of 2-3% from December to April and 20 h males had GSI values of 2-6% from December to August. This indicates, in contrast to female suppression, male gametogenesis and investment in gonadal development at 20 h was not inhibited in the second year. Immature and post-spawning males had GSI values of <1% across all treatments.

Summing up, gonadal investment, as measured through GSI, revealed that females invested ~8% of their body weight in gonadal mass and males ~4% on average (based on pre-spawning, non-ovulated ovaries and ripe pre-spawning testes of males that did not expel milt, adult data on all treatments pooled). The mass of hydrated gonads in spawning condition is higher and consequently these constitute higher GSI values than pre-spawning gonads (Figs. 13 and 15). The GSI of immature cod of either sex was <1%. Depleted gonads (post-spawning) were characterized by a GSI of 2-3% for females and 1-2% for males. Partly hydrated ovaries of spawning females exhibited the highest gonadosomatic index with mean values commonly attaining 13-18%, whereas the GSI of spawning males was often between 4-7%.

PERCENT WATER CONTENT OF MUSCLE

Kelly Cove Site

In Kelly Cove, percent water content of muscle tissue of females commonly ranged from 78-81% for NP and 24 h light treatments (Fig. 16). Spawning females interestingly exhibited the highest moisture contents of fillets with values often ranging from 85-95% and represented increases of 5-10% over pre-spawning and post-spawning females. Water content of muscle of immature females ranged from 78-84%.

Similar to females, percent water content in muscle of males ranged from 78-81% for both NP and 24 h light treatments (Fig. 16). Unlike females, however, there was no noticeable increase in water content of fillets for spawning males.

Fundy Site

In Fundy site, percent water content of muscle tissue of adult females commonly ranged from 78-83% for NP and the 20 h light treatment (Fig. 17). Spawning females for the most part exhibited the highest water content but only marginally (by ~2-3%) over other adult females. Water content of muscle of immature females ranged from 80-83%.

Percent water content in muscle of adult males ranged from 78-82% for NP and the 20 h light treatment (Fig. 17). Unlike for females, immature males had higher muscle water content (i.e., 82-86%) compared to mature males. Males at spawning, unlike females, did not exhibit higher water content in muscle compared to the non-spawning condition.

PERCENT WATER CONTENT OF LIVER

Kelly Cove Site

In Kelly Cove, percent water content in liver of adult females ranged from 25-35% (Fig. 18). There was a large degree of similarity in values within a sampling period among different gonadal stages (as noted by low standard error values). In general, water content was higher in winter/spring than in summer. Water content was 5-10% lower in livers of immature compared to adult females. At 24 h light, percent water content was stable from 22-27% from January-June and then increased slightly in the autumn and further into the winter/spring spawning period followed by a decline during the second summer.

For NP males of Kelly Cove, percent water content of liver of males was similar to that of females but with greater variability and ranged from 20-35% (Fig. 18). For 24 h males of Kelly Cove, variability was low and at similar levels to females. Values ranged from 22-33% with an increase in water content as the season passed from fall into winter-spring and then declined in summer in the second year.

Fundy Site

In Fundy, percent water content of liver of NP adult females ranged from 35-50% (considerably more than for their counterparts at Kelly Cove) (Fig. 19). The single immature female sampled at NP was 24%. There was no marked seasonal trend in percent water content in the first year though a slight decline to 35% was noted in the second summer of sampling. At 20 h light, percent water content ranged from 33-48% with post-spawning females exhibiting the greatest moisture content and immature females the lowest. Post-spawning males exhibited in general the greatest liver water content at each sampling. Lower values tended to occur during the summer period and higher values in the winter/spring.

HEPATOSOMATIC INDEX

Kelly Cove Site

The hepatosomatic index of NP adult females ranged widely from 5-12% (Fig. 20). Values were higher in the winter/spring period compared to summer. Immature females exhibited hepatosomatic index values of 3.5-5% and were the lowest of all gonadal stages. At 24 h light, the hepatosomatic index of adult females ranged from 6-12% with a more pronounced summer decline in HSI compared to NP females as HSI declined from 12 to 6% from February to September 2006 and then began to increase to 8-10% by winter/spring of 2007. For immature 24 h females, their values were very similar to adult females in winter/spring 2006.

The hepatosomatic index of NP adult males ranged from 6-10% (Fig. 20). A decline in HSI was noted from winter/spring through to fall in 2006 followed by an increase the following winter and another decline into summer 2007. At 24 h light, HSI of males ranged from 4-12% with a decline noted from winter/spring through to fall (similar to that noted for females of this same treatment). There was no particular trend in value of HSI in relation to gonadal stage of development.

Fundy Site

The hepatosomatic index of NP adult females ranged from 4-12% with the highest value occurring in December 2008 (immature females were <2%) (Fig. 21). At 20 h light, HSI of adult females ranged from 4-10% with a decline noted from winter through to summer (immature females had the lowest values of HSI). In the second year of cage illumination the hepatosomatic index was lowest at 20 h (~6%) compared to fish held at NP.

The hepatosomatic index of NP adult males ranged from 4-9% with values near 8% occurring from December 2008 to August 2009 (immature females were <3%) (Fig. 21). At 20 h light, HSI of adult females ranged from 5-8% with no large seasonal changes over the duration of the trial. Immature males exhibited both the lowest and the highest HSI values.

DISCUSSION

Continuous light has been previously demonstrated to improve somatic growth of fish held in sea cages and in the laboratory for a number of fish species including Atlantic salmon (Hansen et al. 1992, Harmon et al. 2003), turbot (*Scophthalmus maximus*) (Imsland et al. 1997; Imsland and Jonassen 2003), Atlantic halibut (*Hippoglossus hippoglossus*) (Imsland and Jonassen 2005), gilthead sea bream (*Sparus aurata*) (Kissil et al. 2001), sea bass (Rodríguez et al. 2001), haddock (*Melanogrammus aeglefinus*) (Trippel and Neil 2003) and Atlantic cod (Dahle et al. 2000; Hansen et al. 2001; Skjæraasen et al. 2004; Karlsen et al. 2006; Taranger et al. 2006). A similar positive growth response to extended daylength was observed in the present study. Immature cod of each gender in our study were reported to attain smaller body sizes than mature cod and this trend was consistent across all treatments and multiple years. This result is a bit puzzling as one would predict that animals not undergoing gametogenesis would have more energy available for somatic tissue development and hence body growth (Bell 1980). However, increased appetite in relation to sexual maturation is often overlooked in growth-reproductive studies. It may be that the appetite of immature fish is poorer than of maturing fish and so ration size (i.e., daily amount of food consumed per unit body weight) was much less for immature fish. Sometimes immature fish only weighed one-third of mature fish. This trend of smaller immature compared to mature individuals was also reported of same-age fish in populations of plaice (*Pleuronectes platessa*) and cod (Rijnsdorp 1993; Trippel et al. 1995). Applications of life history theory that predict a somatic cost of reproduction (Reznik 1992; Kozlowski 1992; Hutchings 1999) need to be cognizant of the improbability of one of their key underlying assumptions; that the appetite and annual food intake is equal among population members of a cohort. Growth of maturing male Atlantic salmon parr was faster than of non-maturing parr (Rowe and Thorpe 1990) and maturing fish grew faster than immature fish in both sexes of

white sucker (*Catostomus commersoni*) (Trippel and Harvey 1989). Moreover, feeding habits and intake were reported to be inferior in immature compared to maturing Atlantic salmon (Kadri et al. 1996). Thus, one aim of our study to generate immature cod to improve somatic growth was not supported by our findings. Further study of this concept is required with greater sample sizes of fish and where possible seasonal assessment of appetite in relation to maturation and spawning throughout a year and multiple years.

Twenty-hour and 24 h light treatments did not influence the incidence of sexual maturation of females and males in our study. The greater light intensity used at the Fundy site also did not serve to reduce incidence of maturity. Proportion of fish sampled that were mature was often >90%. In other species, like Atlantic salmon, use of continuous light has been successfully applied to stop or reduce the incidence of sexual maturation in sea cages (e.g., Harmon et al. 2003) and in tanks (e.g., European sea bass (*Dicentrarchus labrax*) (Begtashi et al. 2004) and gilthead seabream (Kissil et al. 2001)). In the Bay of Fundy, in 70 m circumference polar circle cages containing Atlantic salmon only two 400 W lights per cage are necessary to halt gametogenesis such that Cooke Aquaculture Inc. noted a reduction in incidence of sexual maturation from 4-10% to <1% per cage (R. Griffin, pers. comm.). Percentages of mature salmon in lit cages (female 0.3%, male 2.1%) were lower than in unlit control cages (female 9.0%, male 47.0%); these results are for when two 400W *SeeBrite*™ lights per 12.7 m diameter sea cage were turned on in November (Peterson and Harmon 2005).

Implementation of 24 h light did, however, result in delaying attainment of complete sexual maturation of Atlantic cod (i.e., ovulation and milt release) by ~3 months into summer at Kelly Cove in the first year of exposure and this retarding influence was most pronounced for females. Maturation, however, returned to more normal winter/spring timing after the second winter of light exposure. Thus, 24 h light treatment was having some effect, but not sufficient to produce the intended output of immaturity.

In the Fundy site, 20 h light was more effective than ambient light in suppressing reproductive investment of maturing fish as represented by the gonadaosomatic index. That is, the fish that did mature had very small gonads at 20 h light, particularly after two winters of light exposure. Consequently, 20 h light may hold promise as a method of suppressing the energetic investment in reproductive tissue, with less financial expenditure to power lights, enabling more of the food energy to be allocated to muscle. It is uncertain why 24 h light was more effective in the first year of the Kelly Cove study, and 20 h was more effective in the second year of the Fundy site study. The different 'natural' spawning times of the parents of the fish used in the two trials (Kelly Cove, June spawners; Fundy site, December spawners; G. Nardi, pers. comm.) also adds some complication to the interpretation of the results (Otterå et al. 2006). Light intensities also differed between sites. Consequently, within-site comparisons are the most appropriate to be made within this study. The economy of running 20 h vs. 24 h light treatments is also worth consideration. At 45°N, darkness in the third week of December lasts ~15 hours and in mid October ~13 hours. Thus electricity charges would be reduced at the winter solstice by 27% and the percent saved would increase as the days shortened. It would also be worth exploring whether lights could be turned on in autumn and off in spring as is done for salmon cages. We also encourage salmon farmers to examine 20 h as an alternative to 24 h light.

The mechanism by which 20 h light acts and possibly is more effective than 24 h is as follows. Given that the pineal organ of cod is very light sensitive relative to salmon, it may be possible that at 24 h light cod are sensing the shortening of daylength in autumn (Porter et al. 1999, 2000). This may be because daylight intensity is much stronger than that emitted by artificial light fixtures thereby leading the pineal-sensitive cod to cue on these natural light/dark rhythms. Even by generating 4.8 kW per cage it was still apparently insufficient to mask the animals' perception of natural changes in daylength, as fish exposed to 20 h light exhibited a high incidence of sexual maturation. The modest gonadal development in the second year of implementing 20 h light at the Fundy site may have been a result of animals cueing on the 20 h light and 4 h dark to a greater degree than natural seasonal changes in diel light levels. Animals at 20 h light would have been exposed to three different light regimes, sometimes referred to as a "skeletal photoperiod", (Kissil et al. 2001): natural daylight and its inherent changes over the day, the dimmer artificial illumination from sunset to midnight, and then, unlike the 24 h light treatment at Kelly Cove, they were exposed to an unchanging period of 4 h darkness. It may be that this fixed 4 hours of darkness that occurred daily partly 'masked' a cod's ability to recognize the shortening of days in autumn. In captive experiments, administering 16 h daylength resulted in a decreased incidence of first sexual maturity of male turbot (Imsland et al. 1997) and 15.5 h daylength caused a delay in sexual maturity of both sexes of gilthead seabream (Kissil et al. 2001). Further research at cage sites is recommended to explore this option with more replicates and intensive sampling. Ideally, unchanging light intensity through a 24 h period is desirable, though this is apparently not a prerequisite to successful inhibition of sexual maturation of Atlantic salmon held in sea cages as light intensities from sources of 0.8 kHz per cage would have generated much lower light levels than in the present study (Hansen et al. 1992; Harmon et al. 2003; Porter et al. 1999).

Water content of fillet muscle was surprisingly quite constant throughout the study with only minor variation. Hence, cod of the body size examined in this study apparently maintained water content of fillets and only during the spawning period was the quality of the female fillet compromised (occasionally higher by 5-10% at Kelly Cove and 2-3% at Fundy site). Rapid ingestion (i.e., hyperphagia) of large quantities of food by post-spawning females (Fordham and Trippel, 1999) may partly account for the rapid re-conditioning of muscle. The high availability of food in sea pens presumably differs from fish in the wild which may be exposed to poor foraging conditions post-spawning which prolongs poor body condition; e.g., a 4% elevated water content of fillets was observed for large-bodied, spawning compared to non-spawning female American plaice (*Hippoglossoides platessoides*) (Templeman and Andrews, 1956). Muscle water content rose by 5% in spawning Atlantic cod collected off Nova Scotia (Dambergs 1964); of interest is this report also noted decreases in fat (-20%) and protein (-5%) and an increase in water solubles (+10%) which comprise a complex mixture of free amino acids, water-soluble vitamins, various nitrogenous bases, and other comparatively low molecular weight organic compounds found in muscular plasma. In the Balsfjorden of Norway, the increase in gonad mass of cod from January until spawning accounted for ~33% of the energy decline in the muscle (Eliassen and Vahl, 1982). Consequently, our documentation of water content, although of interest, does not fully reflect the nutritive deficiencies that co-occur with 'jellied' fillets of spawning female cod.

Investment in liver tissue was greater in female than male cod as has been reported previously (Dahle et al. 2003; Solberg and Willumsen, 2008). In our study, there was a tendency for the hepatosomatic index to be greatest during the winter/spring period and for pre-spawning fish. Investment in liver tissue was lowest for immature fish. These trends support the important role liver plays in storing and diverting lipids to the gonad. The greater water content of liver post-spawning is also of interest. In captive cod in Norway, the hepatosomatic index was highest just prior to spawning for females and males (Dahle et al. 2003) and is consistent with the results of the present study. Karlsen et al (2006) observed the lowest liver weights during spawning in both sexes. It is clear, with changes in mass and composition of organs, that since little is eaten during spawning, female cod must mobilize energy from the muscle via the liver to the ovary.

Extended photoperiod resulted in delaying sexual maturation of Atlantic cod to a period when water temperatures were warmer. Spawning of eggs in warmer water might possibly reduce their potential to be fertilized and survive compared to those spawned in more normal cooler water. Thus, in this way, the use of lights may act to mitigate against the spawning and survival of embryos generated by mating cod in sea cages (Jørstad et al. 2008). Furthermore, farmed cod that escape which had been exposed to prolonged daylength may also be a less serious threat than those maintained at natural photoperiod (Meager et al. 2010) as asynchrony in gonadal maturation among farmed and wild cod would be expected, at minimum for within a year after escape.

Spawning mortality of cod in cages is believed to be quite high, particularly among females over age 3 years, > 60 cm length (L. Dickinson, pers. comm.) and was recently confirmed in laboratory studies in Iceland (Árnason and Bjørnsson 2011). The fact that 20 h light impeded gonadal investment may reduce the likelihood of mortality associated with the 'egg bound' state, however, light treatments also tend to postpone maturation and the 'egg bound' state could occur during a period of warmer summer temperature which may lead to added physiological stress for these burdened females. It would be expected, however, that females with a small ripe ovary may not suffer so much from 'egg bound' related mortalities (mortality is likely highly correlated with GSI and if gonad investment is low one would expect mortalities to also be low). Hence, the effect of extended daylength on mortality of Atlantic cod in sea cages requires further investigation.

More effective suppression of maturation was observed when using photoperiod treatments in enclosed tanks than in sea cages (Porter et al. 2000; Davie et al. 2007). Presumably, this is due to using "light-tight" lids which prevent fish from the opportunity of perceiving diel changes in natural daylength. Cages in our trials were not covered with a shade cloth and even if they were there would still have been ample opportunity for cod to sense diel changes in daylength. The difficulty in using artificial illumination to impair reproduction in cod encourages investigators to explore alternative means to reduce the incidence of sexual maturation. A simple method to generate sterile fish is the induction of triploidy by use of embryonic hydrostatic pressure treatments within a few hours post fertilization. This approach appears to show some merit for cod and is worthy of exploration (Perruzi et al. 2007; Trippel et al. 2008; Feindel et al. 2011) and also would aid in reducing the chances of genetic introgression between wild and cultured cod (Feindel et al. 2010). Twenty hour light exposure, nonetheless, should be explored further for Atlantic cod and Atlantic salmon mariculture. The interesting observation of poor growth of

immature cod, however, indicates that further research is necessary to evaluate the somatic cost of reproduction, perhaps via the development of sterile triploids since the number of large-bodied, immature cod obtained via cultivation is rather limited due to the high incidence of puberty.

Artificial light extending beyond the periphery of the sea cage was noted and is of interest from an environmental light distribution perspective (Trippel 2010). However, light intensity did not exceed 21 lux along the insides of the cage sides and was reduced to negligible levels ($\leq$1 lux) at 2 m outside of the cage sides (Table 2). Interestingly, the highest peripheral light intensity (271 lux) existed at the bottom of the sea cage at the Fundy site (when using 4.8 kW light intensity). Since the cage bottom was ~10 m above the ocean floor, the amount of light passing through the sea cage bottom mesh would have extinguished well before reaching the ocean bottom. If the cage net was situated in shallower water there could have been some light penetration to the sea floor. Noteworthy, however is that the amount of light used in this study was much greater than is routinely used to suppress maturation of Atlantic salmon (0.8 to 1.2 kW, Trippel (2010)). We did not measure light intensity in or around salmon cages but based on our measurements it is unlikely that artificial light would reach the perimeter of a salmon cage (given lights are centrally located in a 70 m polar circle cage). Light readings at the cage mesh averaged 2.68 lux in 12.7 m diameter circular cages when lit with two 400 W bulbs which was nearly equivalent to the average of 2.15 lux in an unlit cage (Harmon et al. 2003; Peterson and Harmon, 2005; Trippel 2010).

The irregular sampling among cages within a treatment for the Fundy site was a disadvantage in the execution of this project. If fewer replicates had been monitored at the onset of the second trial, there could have been more intensive monitoring of individual cages over time. As mentioned previously the lack of replication in sea cage photoperiod trials has been encountered in a number of reports, as noted in the Kelly Cove trial. Despite these deficiencies, our results suggest the use of extended daylength to improve growth and change the timing and investment in reproduction holds some promise for Atlantic cod mariculture.

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FIGURES

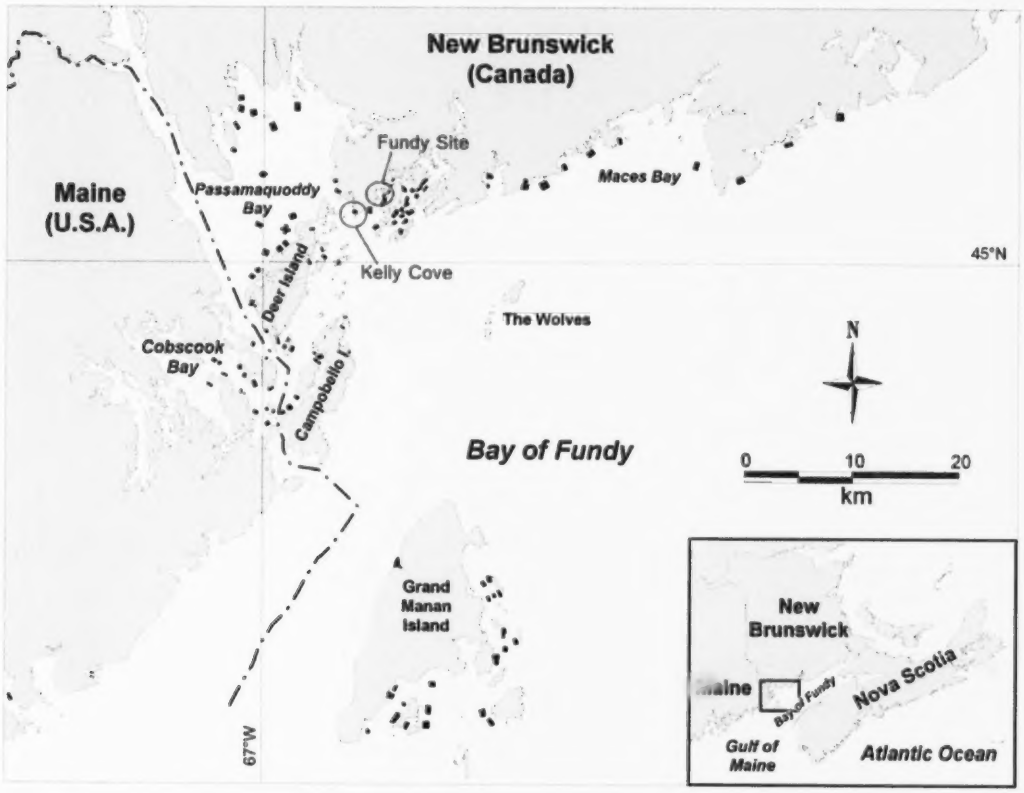

Figure 1. Map showing Bay of Fundy with the locations of two cod aquaculture sites (Kelly Cove site (2005-2007) and Fundy site (2007-2009)) operated by Cooke Aquaculture Inc. at which the study occurred.

Figure 2. Aerial photo of cod aquaculture site located near L'Etete Passage (Green Point Lighthouse referred to as "Kelly Cove site".

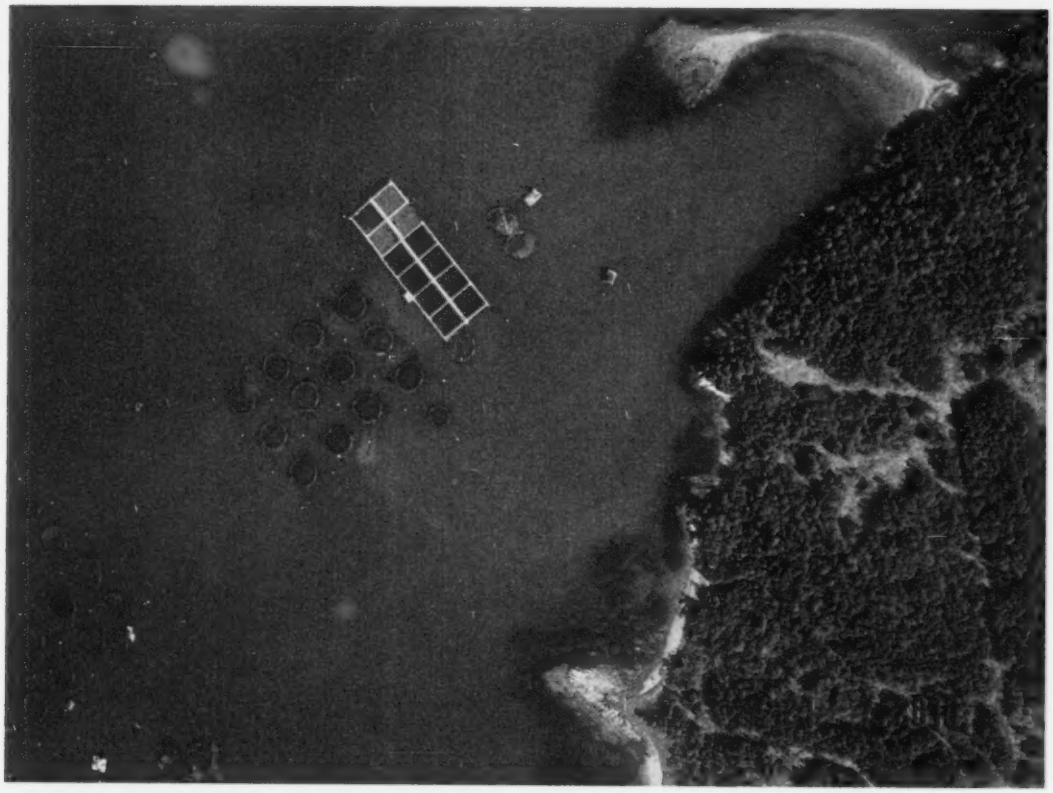

Figure 3. Aerial photo of cod aquaculture site near Back Bay, New Brunswick referred to as "Fundy site".

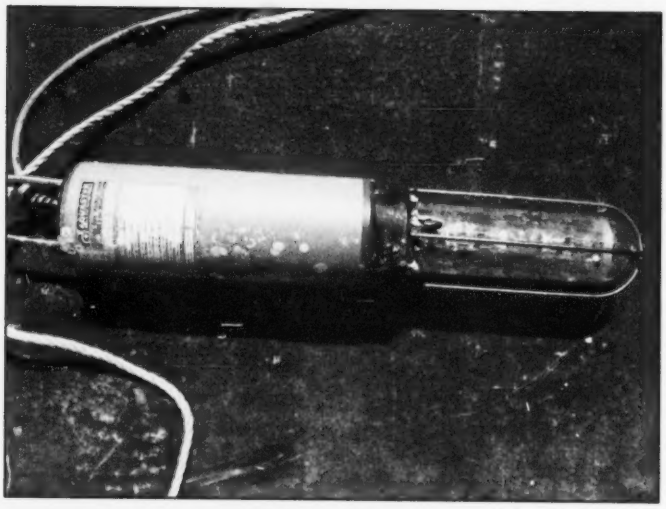

Figure 4. Aquastar aquaculture machine systems, submersible photoperiod lighting 800 W 220V-50HZ bulb type: halogen metal with Ignitor 11cm diameter 100cm length, bulb life: 12,000 h, colour yield- 90 CRI colour temperature: 6500 degrees K glass type: boro silicate. 5mm). Six of these were used in a 70 m polar circle cage holding Atlantic cod in the Bay of Fundy, near Back Bay, New Brunswick. Photo credit: O.A. Puckrin.

Figure 5. Photograph at night of a 70 m circumference sea cage holding Atlantic cod in Kelly Cove, New Brunswick (diameter 21.2 m, depth 7.5 m). This cage was lit by six 400W Aquastar submersible lights which were distributed in one horizontal plane at a depth of 2 m such that the six lights were spaced equally apart along the circumference of a 13 m diameter circle pattern centred in the cage. Photo credit: E.A. Trippel.

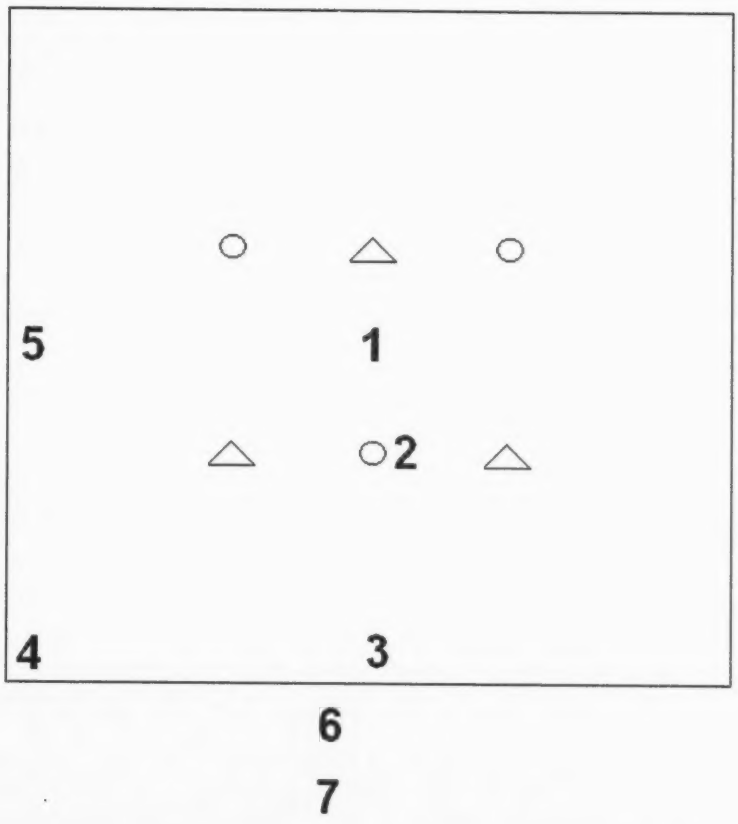

Figure 6. Schematic top view of the lighting array set up in a 20 x 20 m steel cage at Fundy site. Triangles refer to bulbs of upper plane (depth 1.6 m) and circles to bulbs of lower plane (depth 3.6 m). Station 1: center of cage, 2: half-point between two bulbs of upper plane, 3: cage side, 4: cage corner left adjacent to station 3, 5: cage side, 6: outside of cage (2 m), and 7: outside of cage (4 m). See Table 3 for more details.

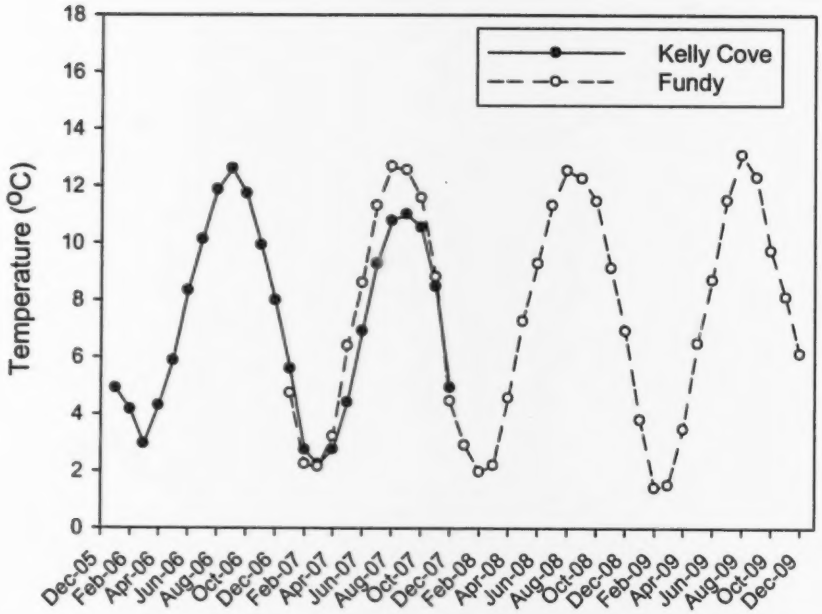

Figure 7. Mean monthly water temperatures (°C) at the Kelly Cove (dark circle, solid line) and Fundy (open circle, dashed line) cage sites for the duration of the study (January 2006-August 2009).

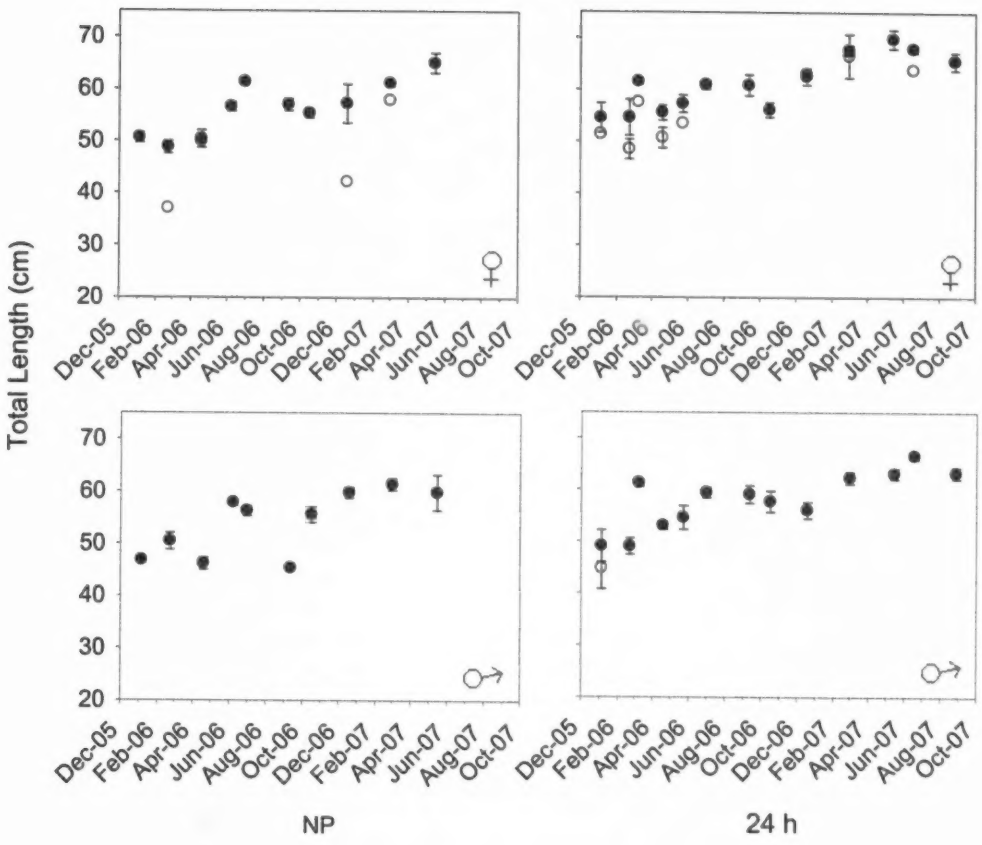

Figure 8. Mean total length (cm) (standard error bars shown) of immature (open circle) and mature (closed circle) female and male Atlantic cod in each of two light regimes at Kelly Cove. Natural photoperiod (NP) and 24 hour light (24 h).

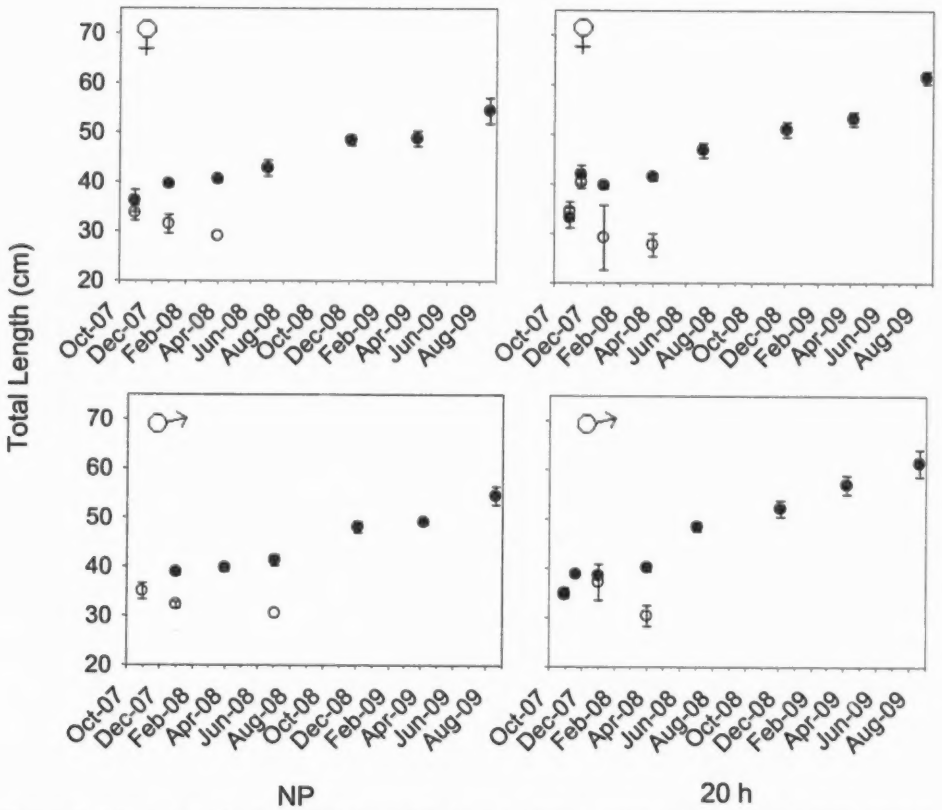

Figure 9. Mean total length (cm) (standard error bars shown) of immature (open circle) and mature (closed circle) female and male Atlantic cod in each of two light regimes at the Fundy cage site. Natural photoperiod (NP) and 20 hour light (20 h).

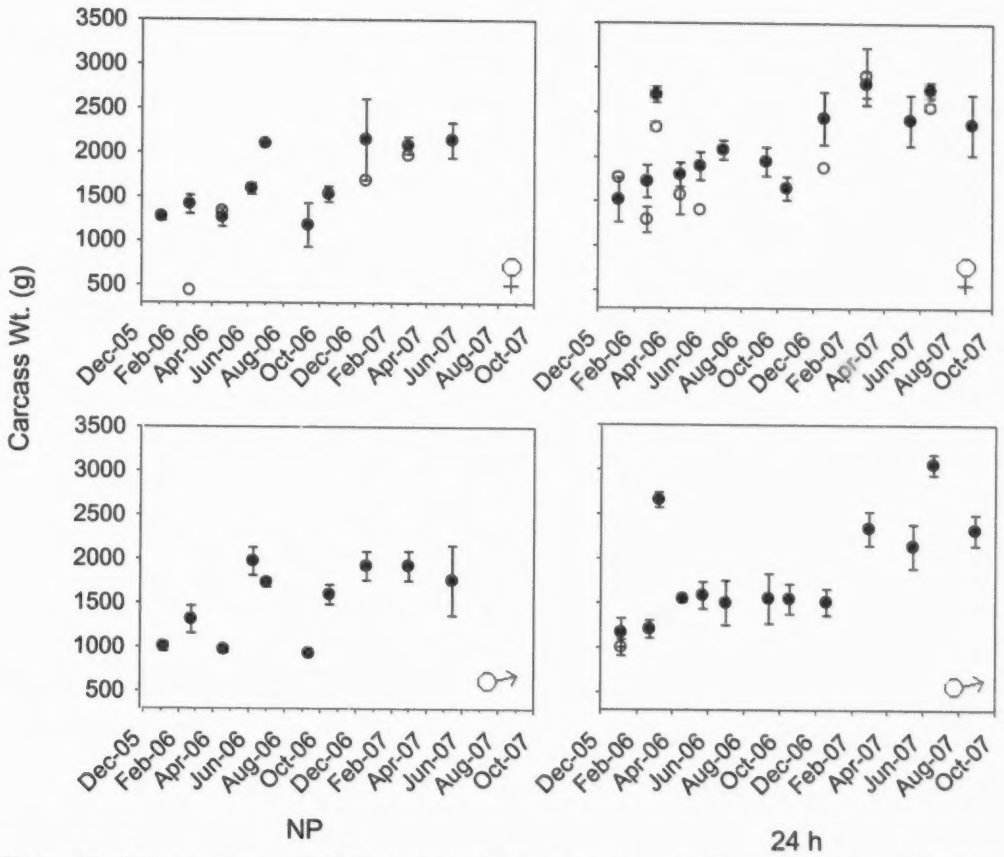

Figure 10. Mean carcass weight (g) (standard error bars shown) of immature (open circle) and mature (closed circle) female and male Atlantic cod in each of two light regimes at Kelly Cove: natural photoperiod (NP) and 24 hour light (24 h).

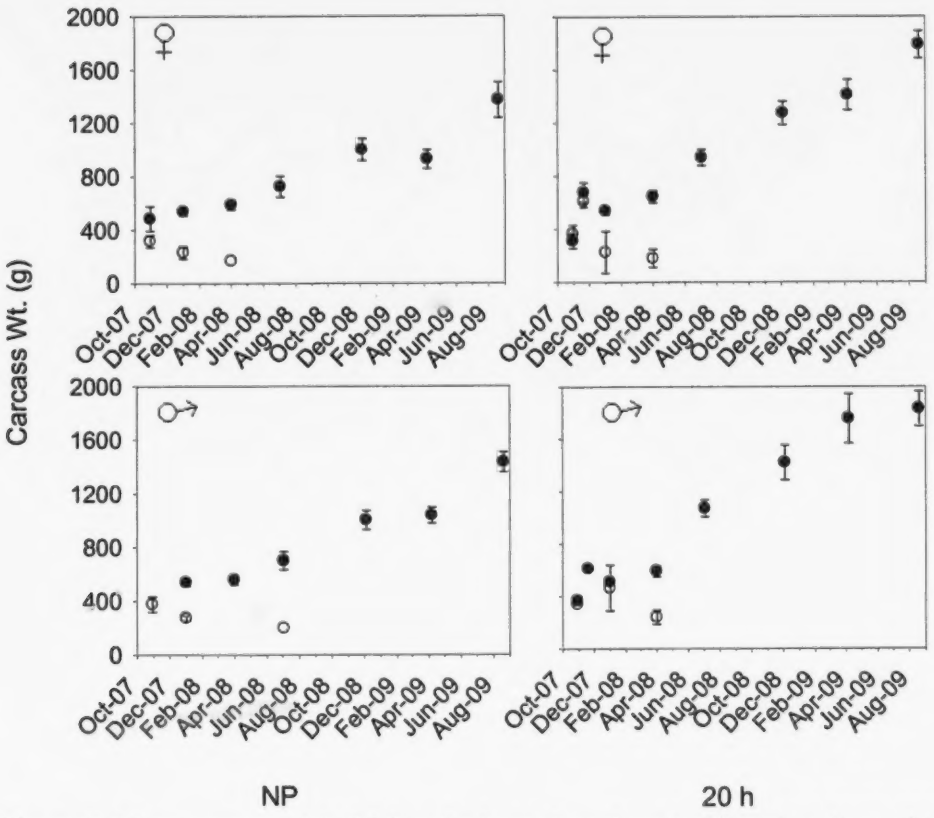

Figure 11. Mean carcass weight (g) (standard error bars shown) of immature (open circle) and mature (closed circle) female and male Atlantic cod in each of two light regimes at the Fundy cage site. Natural photoperiod (NP), 20 hour light (20 h), and 24 hour light (24 h).

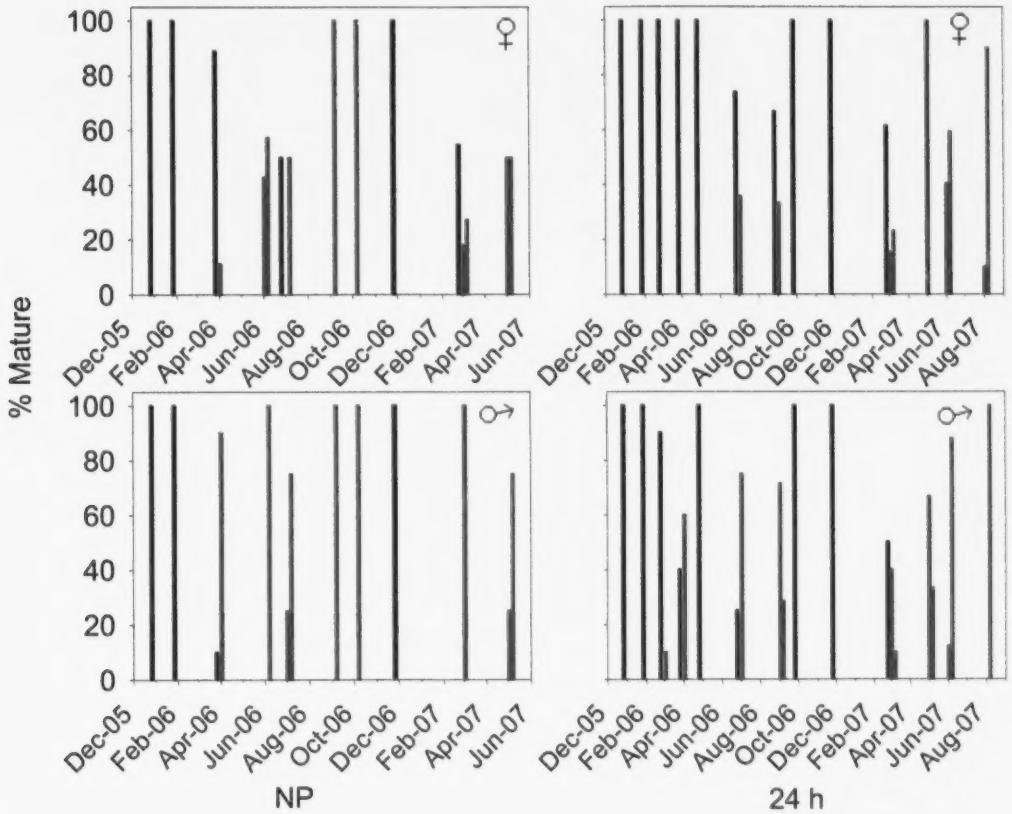

Figure 12. Mean percent occurrence of mature Atlantic cod sampled from each light regime (natural photoperiod - NP, 24 hour light- 24 h) in Kelly Cove classified into 3 categories: ripening: III Rip 1, IV Rip 2 (black), spawning: V Sp 1, VI Sp 2, VII Sp 3 (red), and spent/resting: VIII Reg 1, IX Reg 2, X Deg (grey).

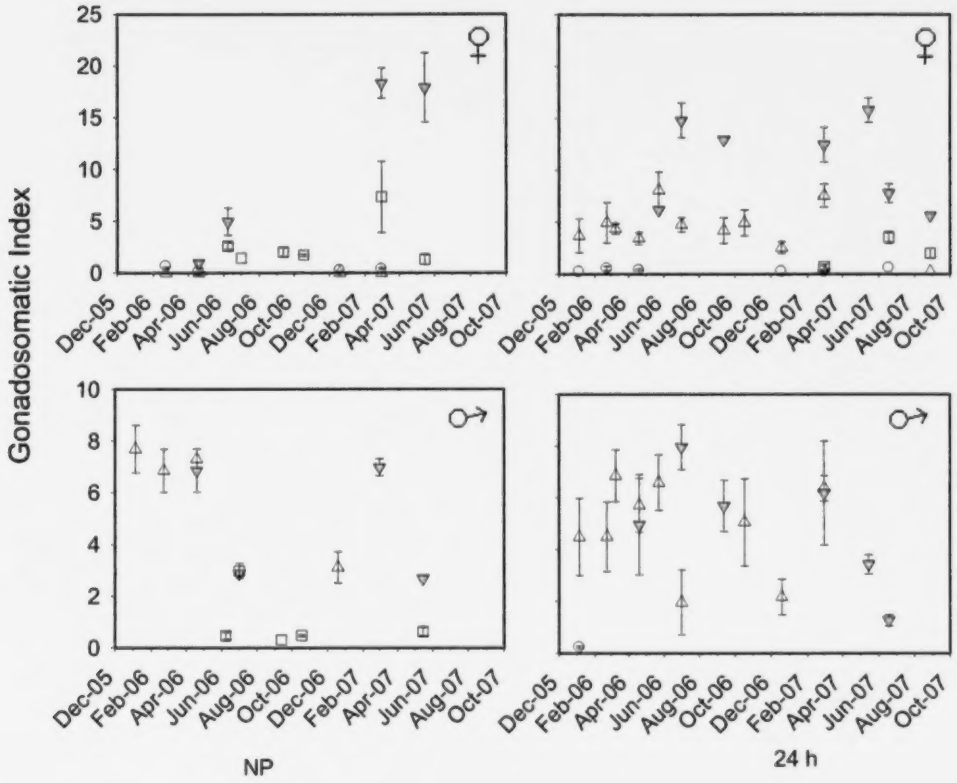

Figure 13. Mean gonadosomatic index (with standard error bars) of immature: I Juv (circle), pre-spawning: II Prep, III Rip 1, IV Rip 2 (upright triangle), spawning: V Sp 1, VI Sp 2, VII Sp 3 (grey inverted triangle), and post-spawning: VIII Reg, 1, IX Reg 2, X Deg (square) Atlantic cod from each light regime (natural photoperiod- NP and 24 hour light- 24 h) in Kelly Cove.

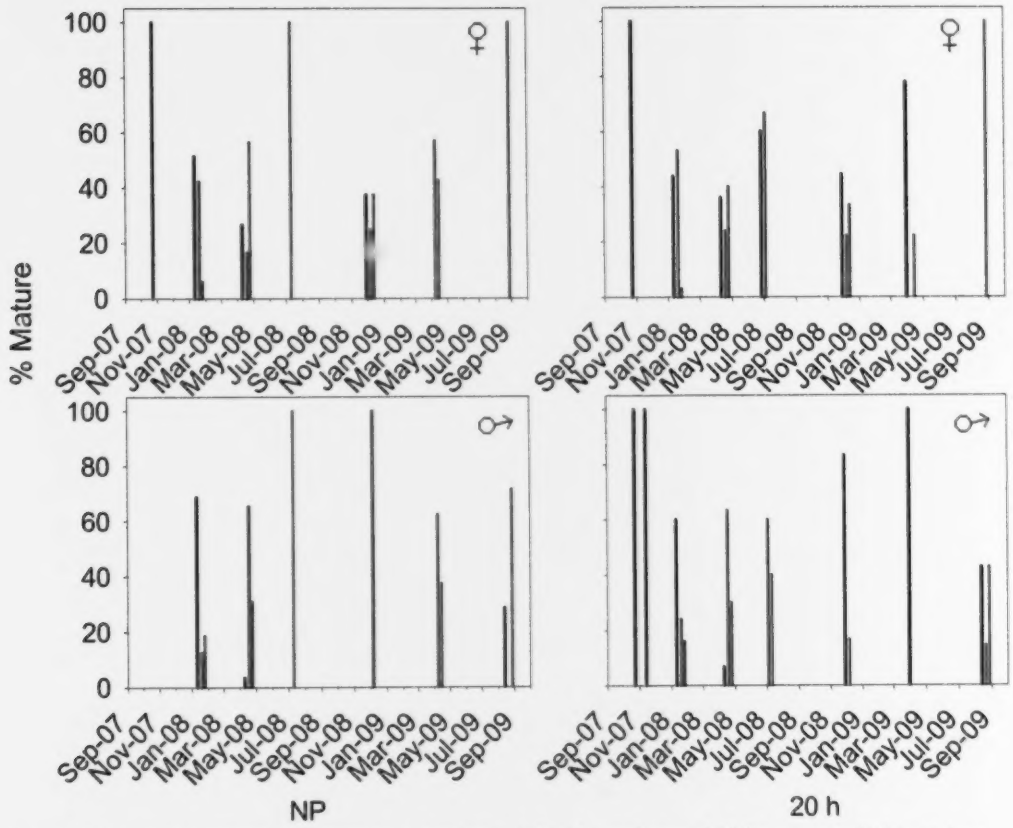

Figure 14. Mean percent occurrence of mature Atlantic cod sampled from each light regime (natural photoperiod - NP, 20 hour light- 20 h) at the Fundy cage site, classified into 3 categories: ripening: III Rip 1, IV Rip 2 (black), spawning: V Sp 1, VI Sp 2, VII Sp 3 (red), and spent/resting: VIII Reg 1, IX Reg 2, X Deg (grey).

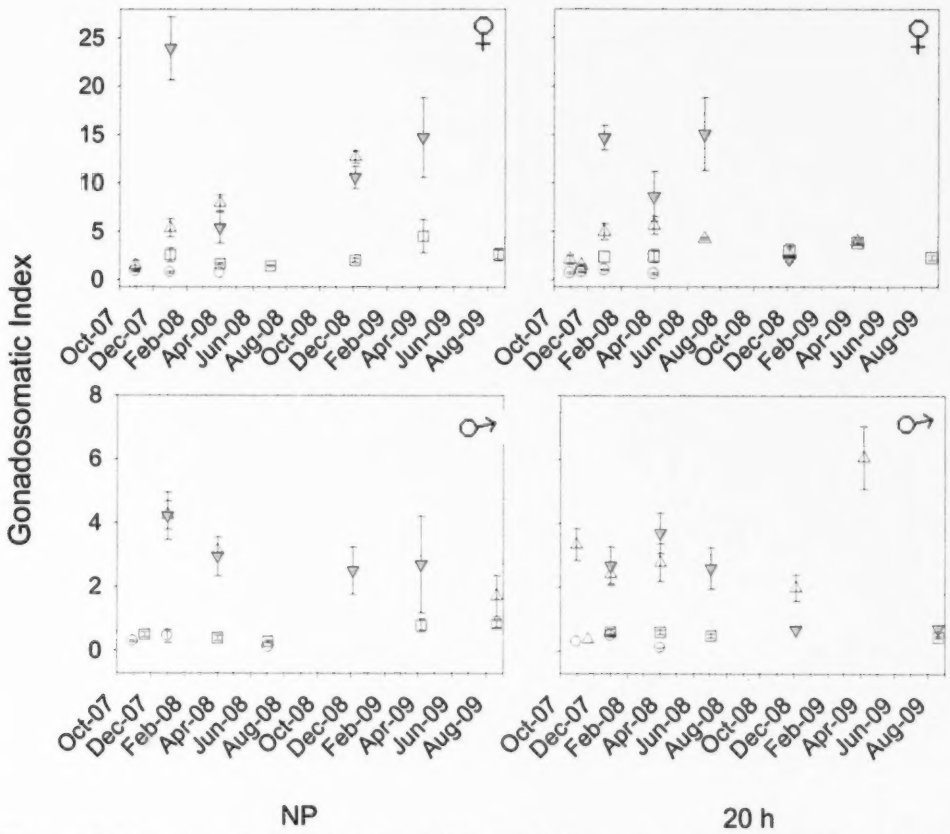

Figure 15. Mean gonadosomatic index (with standard error bars) of immature: I Juv (circle), pre-spawning: II Prep, III Rip 1, IV Rip 2 (upright triangle), spawning: V Sp 1, VI Sp 2, VII Sp 3 (grey inverted triangle), and post-spawning: VIII Reg, 1, IX Reg 2, X Deg (square) Atlantic cod from each light regime (natural photoperiod- NP and 20 hour light- 20 h) in the Fundy cage site, Back Bay.

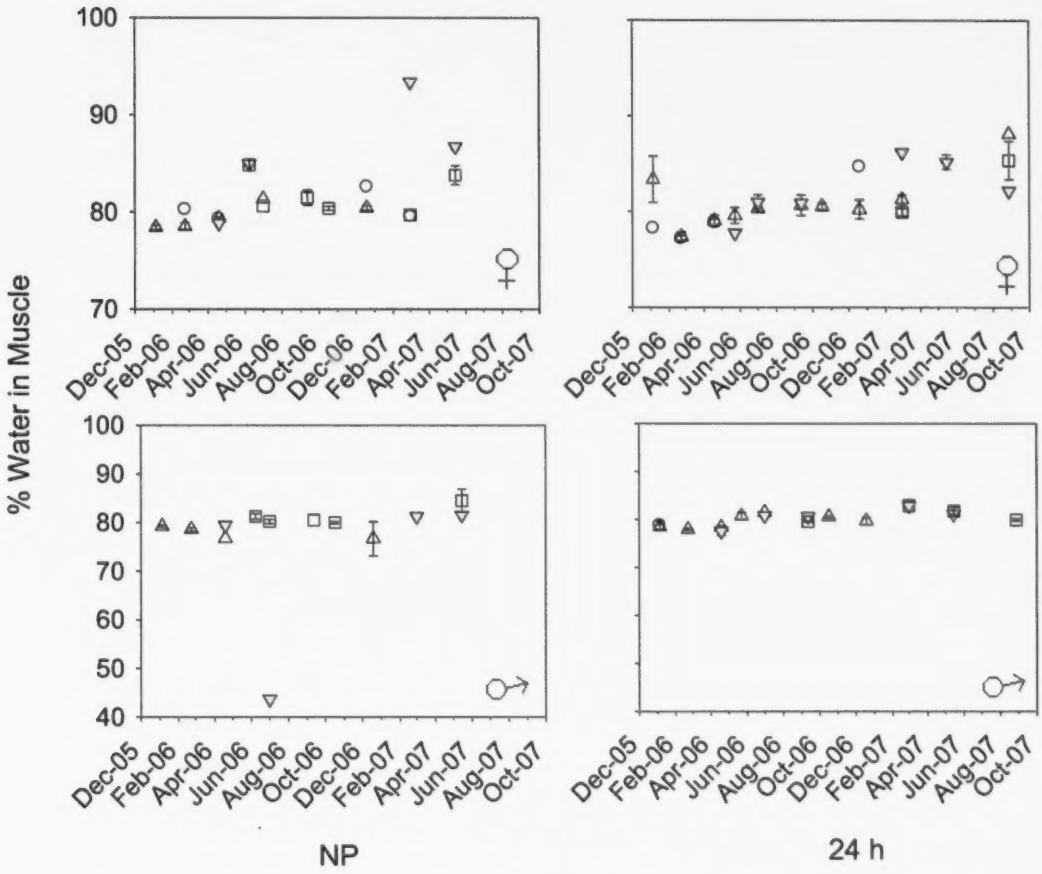

Figure 16. Mean percent water in muscle tissue of immature: I Juv (circle), pre-spawning: II Prep, III Rip 1, IV Rip 2 (upright triangle), spawning: V Sp 1, VI Sp 2, VII Sp 3 (grey inverted triangle), and post-spawning: VIII Reg, 1, IX Reg 2, X Deg (square) Atlantic cod from each light regime (natural photoperiod- NP and 24 hour light- 24 h) in Kelly Cove (standard error bars).

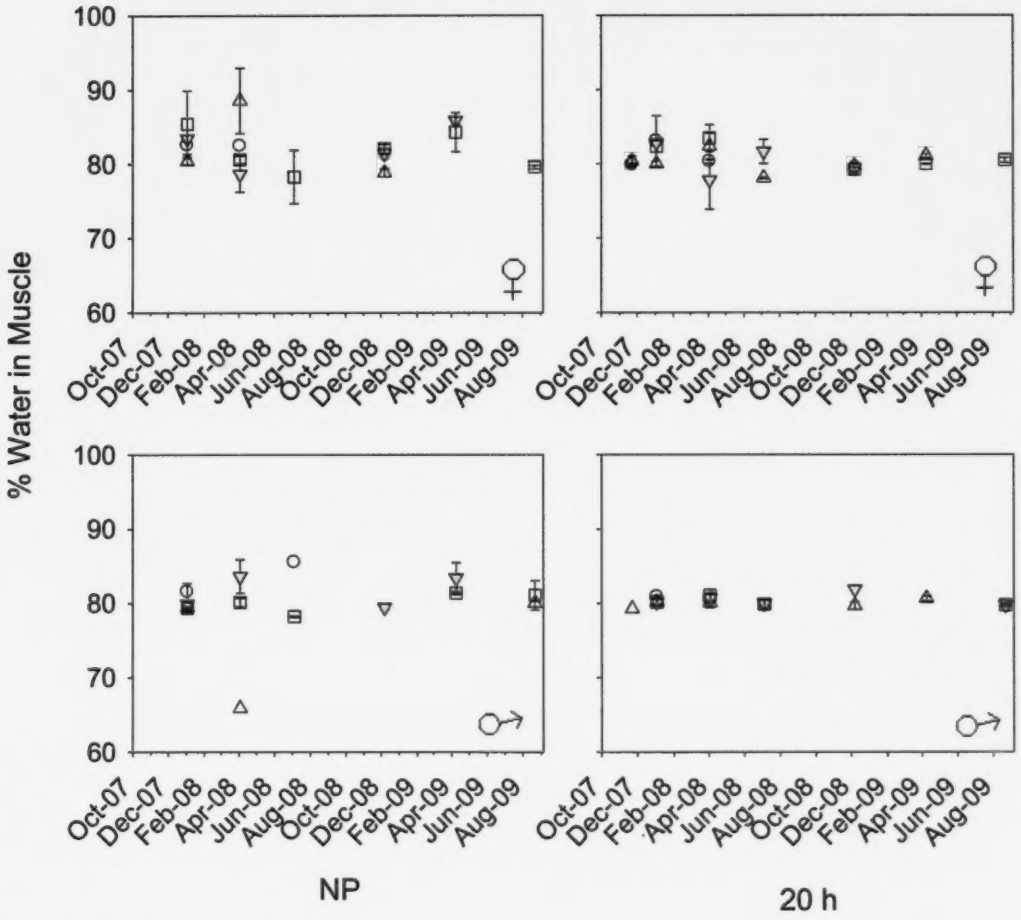

Figure 17. Mean percent water in muscle tissue of immature: I Juv (circle), pre-spawning: II Prep, III Rip 1, IV Rip 2 (upright triangle), spawning: V Sp 1, VI Sp 2, VII Sp 3 (grey inverted triangle), and post-spawning: VIII Reg, 1, IX Reg 2, X Deg (square) Atlantic cod from each light regime (natural photoperiod- NP and 20 hour light- 20 h) in the Fundy cage site, Back Bay.

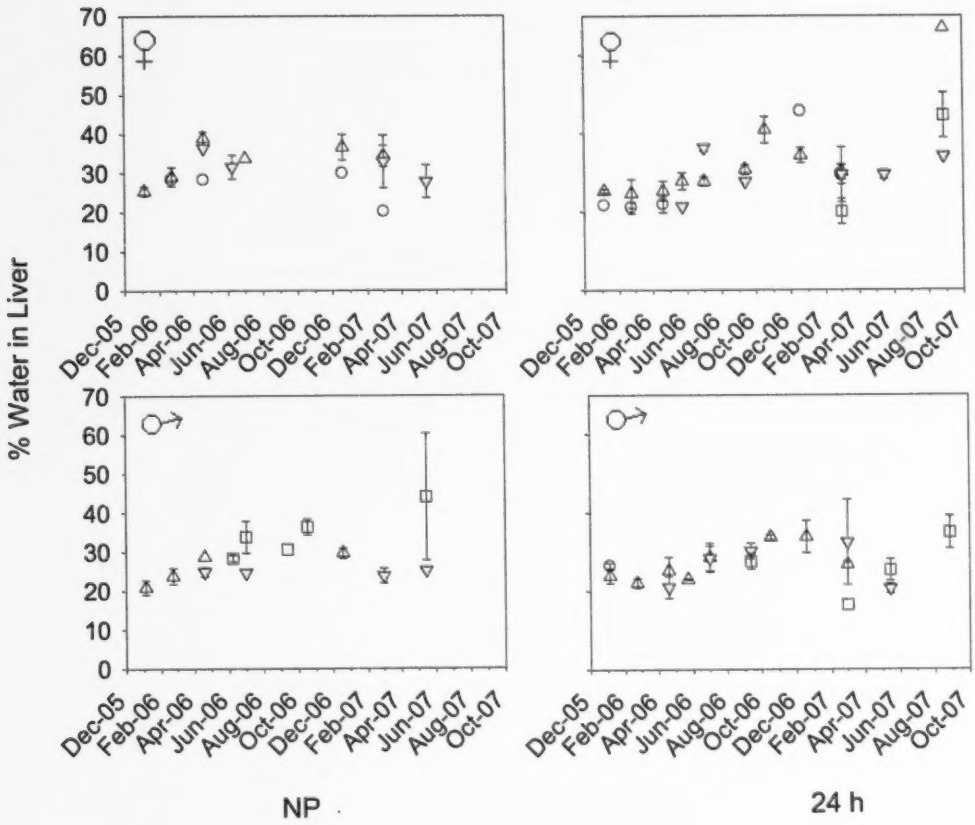

Figure 18. Mean percent water in liver tissue of immature: I Juv (circle), pre-spawning: II Prep, III Rip 1, IV Rip 2 (upright triangle), spawning: V Sp 1, VI Sp 2, VII Sp 3 (grey inverted triangle), and post-spawning: VIII Reg, 1, IX Reg 2, X Deg (square) Atlantic cod from each light regime (natural photoperiod- NP and 24 hour light- 24 h) in Kelly Cove (standard error bars).

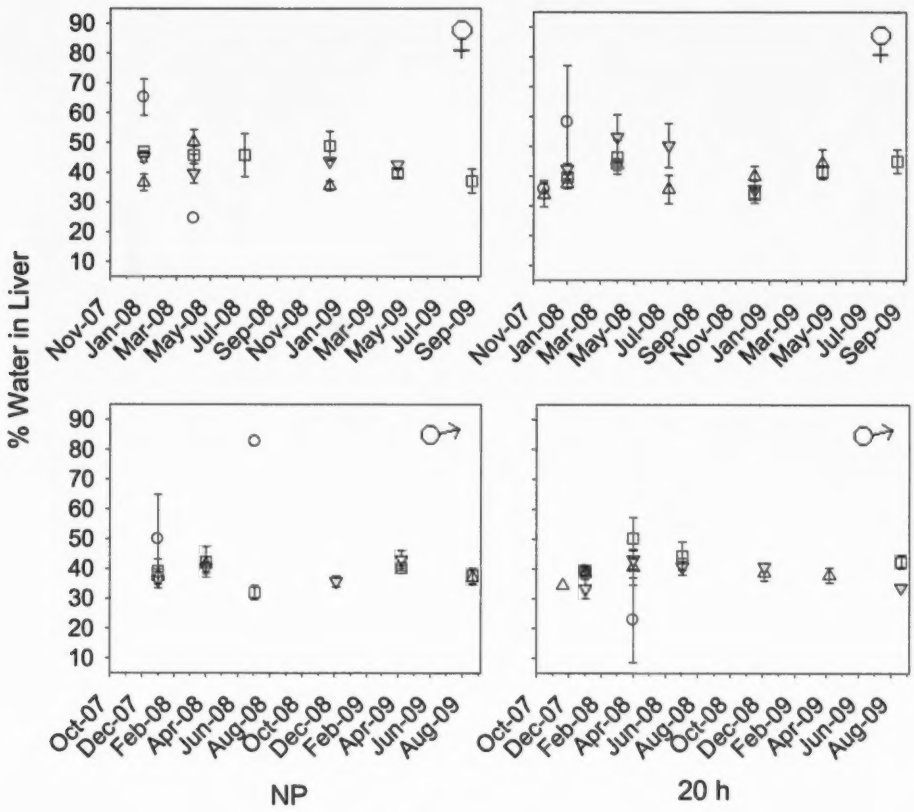

Figure 19. Mean percent water in liver tissue of immature: I Juv (circle), pre-spawning: II Prep, III Rip 1, IV Rip 2 (upright triangle), spawning: V Sp 1, VI Sp 2, VII Sp 3 (grey inverted triangle), and post-spawning: VIII Reg, 1, IX Reg 2, X Deg (square) Atlantic cod from each light regime (natural photoperiod- NP and 20 hour light- 20 h) in the Fundy cage site, Back Bay.

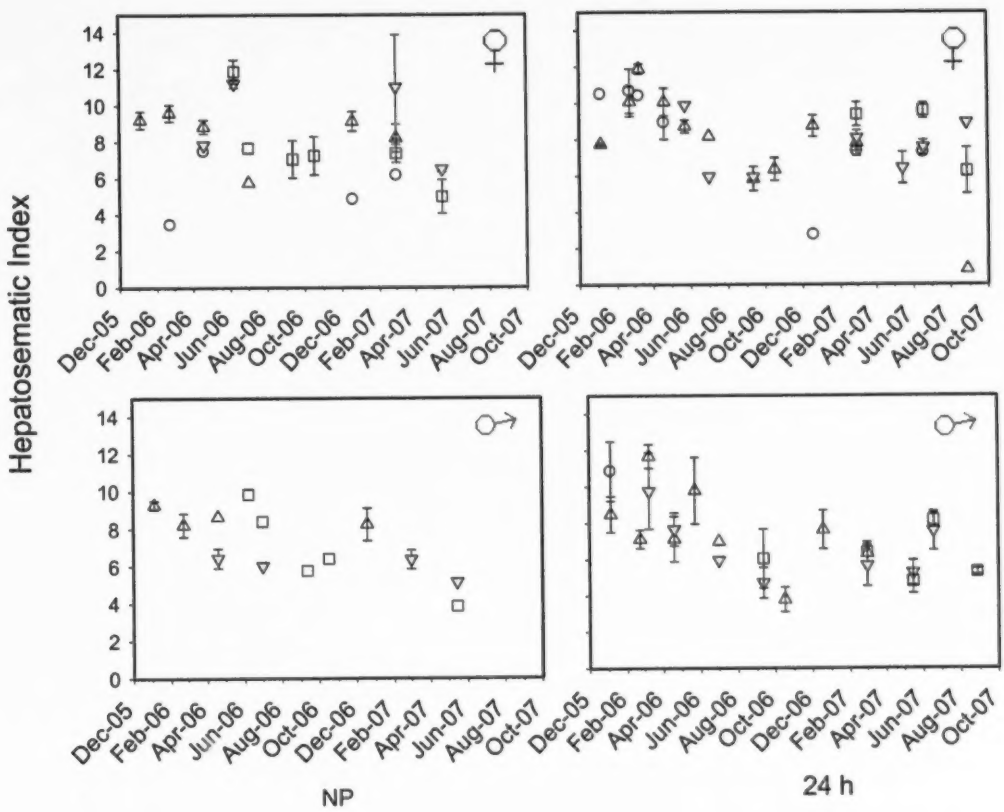

Figure 20. Mean hepatosomatic index (with standard error bars) of immature: I Juv (circle), pre-spawning: II Prep, III Rip 1, IV Rip 2 (upright triangle), spawning: V Sp 1, VI Sp 2, VII Sp 3 (grey inverted triangle), and post-spawning: VIII Reg, 1, IX Reg 2, X Deg (square) Atlantic cod from each light regime (natural photoperiod- NP and 24 hour light- 24 h) in Kelly Cove.

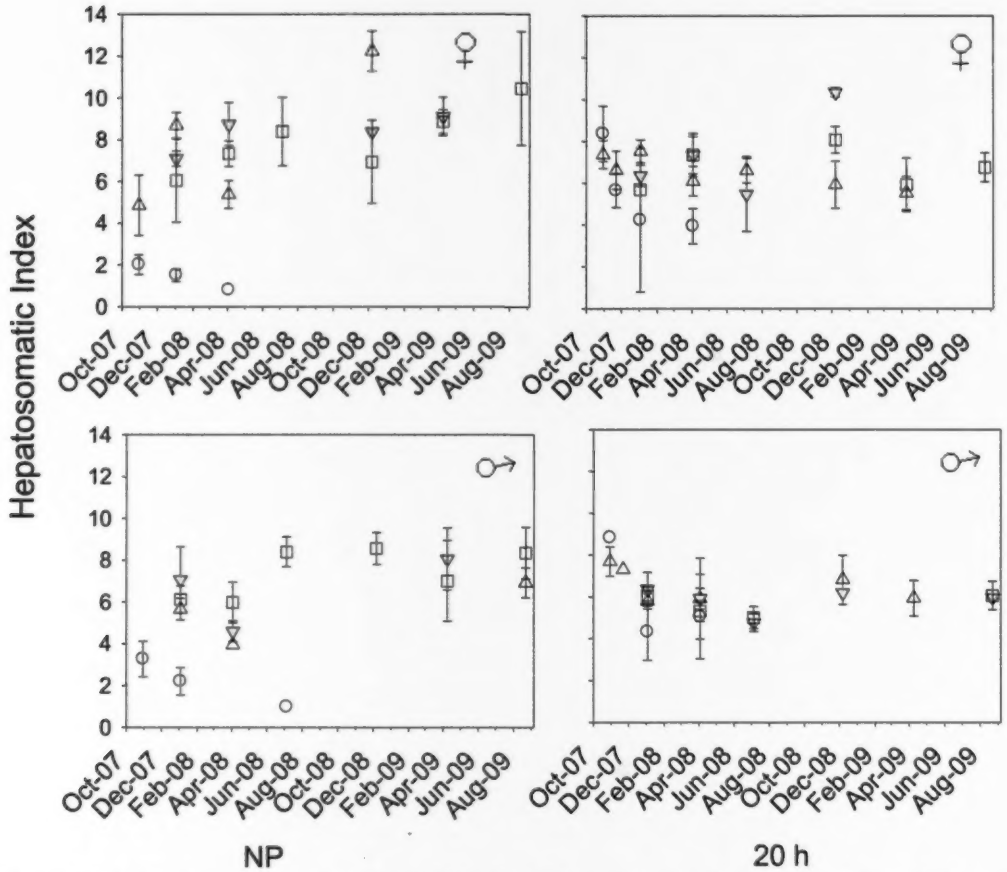

Figure 21. Mean hepatosomatic index (with standard error bars) of immature: I Juv (circle), pre-spawning: II Prep, III Rip 1, IV Rip 2 (upright triangle), spawning: V Sp 1, VI Sp 2, VII Sp 3 (grey inverted triangle), and post-spawning: VIII Reg, 1, IX Reg 2, X Deg (square) Atlantic cod from each light regime (natural photoperiod- NP and 20 hour light- 20 h) in the Fundy cage site, Back Bay.